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# THE PHYLOGENIC STAGE OF THE CAMBRIAN GASTROPODA.

(WITH PLATES I AND II.)

WHETHER it is due to imperfection of the geologic record of the Cambrian age, or whether it is because the class Gastropoda was at that time small and at an initial stage of its differentiation, the species of that age, as known to us, are few, simple-structured, and little diverse, as compared with those of later geologic ages. From the looks of the fossils it might, indeed, be granted that the fauna is both imperfectly represented and primitive. But, as well known, the very simplest and most primitive-looking ones are referable to families the living members of which are believed by zoölogists to be quite remote from the initial or primitive type of the class. If their theory is correct, then the Cambrian Gastropoda must be considered as not near the initial stage of its differentiation, but far advanced, and the Cambrian geologic record as very incomplete. On the other hand, it has not been found explicable why the Cambrian record is so peculiarly and greatly incomplete, and, in short, the primitive looks of the Cambrian Gastropoda are not geologically explained, and the question returns to the interpretation which zoölogists have made of the Recent animal and its shell, whether this is not somewhat at fault for the dilemma. The following paragraphs are intended to offer a concordant interpretation of the geologic and biologic evidence on the Cambrian Gastropoda.

According to the generally accepted view, the gastropod shell, which is the modification of a hollow cone in structure, arose from a symmetrical conical tegulum, and thence the conical, curved conical, spirally coiled, and plane coiled types of shell were successively evolved. The development of the spiral shell has been accompanied by, or has been the cause[1] of, a twisting of the mantle complex of the animal, and since the consequent asymmetrical visceral structure is seen in all Recent Gastropoda, including those which now have simple conical shells and the families to which the simplest Cambrian shells are referable, these appear, because of their visceral asymmetry, to have descended in turn from ancestors which had spirals or coils. Some Recent cones are indeed traceable by fossils to coiled ancestors. The larva, too, of many Recent species has a curved or coiled protoconch or larval shell, and this has been taken as evidence or as proof that the gastropods with conical shells had ancestors with spiral shells.[1] Conical shells may therefore be either the ancestral cones or again the last derived stage in their evolution. One is led finally by the evidence of continual series, apparently, of conical shells from Cambrian to Recent time, to the conclusion that, though they seem primitive, the Cambrian shells are not more so than Recent ones—a conclusion, indeed, which it is difficult to accept in view of the very primitive aspect of the whole Cambrian gastropod fauna; and first of all therefore I desire to emend the theory of the relation of the spiral shell to the visceral asymmetry.

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[1] See ARNOLD LANG, *Lehrbuch der vergleichenden Anatomie* (Zweite Auflage, 1900), pp. 81–7.

## ORIGIN OF THE SPIRAL SHELL.

Known Cambrian fossil Gastropoda are referable to Order I, Prosobranchia, excepting provisionally the Hyolithoidea. Regarding the range of the Prosobranchia, Suborder 1, Diotocardia (Aspidobranchia) includes the group Docoglossa, to which belong Scenella and Patella with conical shells, and these together range from Cambrian to Recent time, without known coiled or spiral ancestor. The group Rhipidoglossa includes some Recent conical shells, Fissurella and Fissuridea, which together range from Carboniferous to Recent, and whose only earlier representatives are coiled, such as Bellerophon and Salpingostoma of Upper Cambrian and Ordovician to Triassic. Suborder 2, Monotocardia (Pectinibranchina), has also simple conical-shaped species, the Capulus of Recent time, and Stenotheca and Platyceras which range from the Cambrian upwards. Of these the earlier ones especially have a short coiled apex.

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[1] See recently, A. W. GRABAU, *American Naturalist*, Vol. XXXVI (1902), p. 918.

The conical shells of other Gastropoda, *i. e.*, those among Pulmonata and Ophistobranchia, are presumably vestigial from spiral ones, and, moreover, are historically distinct from the Cambrian fauna. The Docoglossa are, therefore, seemingly the only ones without known coiled or spiral-shelled ancestor, and any such ancestor must have existed, if at all, before Cambrian time.

The question is, then, whether the Docoglossa had evolved their shells prior to others through all the stages from the primitive conical through the spiral to the derived conical form, or whether they have had no other than the conical shell as yet. It is not necessary to assume that the Docoglossa had a spiral-shelled ancestor. The aspect of the Cambrian fauna, indeed, suggests that such a theory is not the clue to their evolution. And if it could be proved that the Docoglossa had not a coiled or spiral-shelled ancestor, the dilemma could be removed from the interpretation of Cambrian Gastropoda. It seems at least desirable to avoid the set conclusion that the Docoglossa had spiral-shelled ancestors, and this is practicable only by using a conservative view as to the theory of the visceral twisting and by changing the above-cited theory of the spiral-shelled ancestor.

In support of a new theory, it may further be noted here that the Fissurella type of Rhipidoglossa does not appear early enough in geologic time nor in such association as to indicate the probability of truth in the view of the apical slit of its shell[1] having any homology with the similar structure in Dentalium of the class Scaphopoda. The known early Paleozoic gastropods have not even the marginal slit.

Judging from comparison of the living gastropods, it is obviously not to be assumed that the phylogenic groups or lines in which the spiral shell has longest persisted have the visceral asymmetry most strongly developed; but rather the contrary would seem to be the case. It may even be taken that an asymmetrical long cone, while developing phylogenically, was the sufficient cause for the asymmetrical twist of the viscera as seen now in Gastropoda, and that the short conical shell, on the one

[1] *Op. cit.*, p. 83.

hand, and spiral shell, on the other, mark restored equilibrium. A spiral or complete coil may never have existed in the case of the Docaglossa.

### THE TIME SEQUENCE AND FORM SERIES.

If we go back in theory to an ancestral mollusc with solid-layered tegulum, the stages from that to the marginal growth, and consequent hollow enlarged conical shell, seen in the simplest Cambrian mollusc fossils, may be as many as from the latter to the most modified Recent form of it; and the first conical Cambrian shell must well be called gastropod, and considered as far removed from the mollusc common ancestor. How much farther advanced it was may be discussed. Considering that the known Cambrian gastropod shells, in a morphologic sense, may be, some of them, more ancestral or primitive than others, some species or genera should be found among them, as in the later faunas, which were surviving ancient types. Just as the genus Pleurotomaria ranges from Upper Cambrian to Recent time, so also Cambrian genera may have ranged from pre-Cambrian, and the first known fauna may represent an evolutionary series. As said, the long, curved cone is the one which I prefer to consider as the most ancestral type of Cambrian gastropod shell, and the series, on the one hand, to the simple spirals and, on the other, to the short, low conical form, is one-half as long an evolutionary change as from the low conical to the long conical, and to the spiral coil would be. To add, then, from the spiral coil, to the coiled apex, to the secondarily low conical shell, again doubles the length of evolutionary change. In short, the evolutionary series, as represented by the Cambrian fossils, is about one-fourth as long, considering the long curved cone as ancestor of the short cones, as it is if the spiral is taken to precede the derived short cones among Docoglossa.

The time sequence and form series of the Cambrian fossils should indicate the course of development. But that the known Cambrian fauna should not be taken as geologically complete is indicated by the sudden appearance of the first genera. And since the genera known in the Lower pass into the Upper Cambrian, where others suddenly appear, it is necessary, in the interest of fairness, to admit that the other Upper Cambrian genera may have existed in earlier time. This admission breaks the force of argument which otherwise would accompany the comparison of Lower and Upper Cambrian faunas, as a developmental sequence. Yet comparison of the Cambrian fauna with the Ordovician Gastropoda, which are numerous as fossils, is competent to decide whether the Upper Cambrian known types are a fair representation of the marine fauna of that time—which, indeed, they appear to be—and this fauna indicates that the Lower Cambrian known fossils are such as should be expected, provided the group is near its initial, from a long curved conical shell, but that also there may have been many other simple-structured species.

### IMMIGRATION THEORY.

The Baraboo, Wis., fauna is one which contains several gastropod genera whose geologic and biologic relations are, I think, very characteristically Cambrian, and which are of prime importance. This fauna has been described by R. P. Whitfield,[1] and was referred by him to the Lower Magnesian limestone, an equivalent of the New York Calciferous sandrock. It is from an older formation, as indeed suspected from the first, and is in the Potsdam equivalent. C. P. Berkey has found the fauna at Taylor's Falls, Minn., in the Dresbach formation,[2] in the zone of *Lingulepis pinniformis* Owen, with *Lingula ampla* Owen, *Obolella polita* Hall and *Hyolithes primordialis* Hall. These gastropod species, which were first discovered around the Cambrian Islands of the Baraboo region, as well known, recur at the Cambrian shore region about Taylor's Falls, Minn., in the basal conglomerate, and less frequently in the adjacent brachiopod shales. Any considerable geographic distribution of them in the then seaward direction seems to be disproved because, although the Dresbach formation is soon concealed, it emerges at a greater distance around Trempealeau and La Crosse, Wis., and Dresbach, Minn.;

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[1] *Geology of Wisconsin*, Vol. IV., pp. 194–203.

[2] *American Geologist*, Vol. XXI (1898), pp. 270–94.

and there the species of gastropods do not reappear, excepting the *Hyolithes primordialis* Hall. There is, therefore, a good reason for considering the Baraboo gastropod fauna as one occurring only near the Cambrian land, excepting the Hyolithes, which occur also in the normal marine sediments.

This is, I think, the aspect of the known earlier Cambrian molluscan faunas, that Hyolithes and other supposed pteropodous similar genera are common and widely distributed in the marine sediments, and gastropods, Scenella, *et al.*, are rare, local, and probably lived adjacent to land. Their occurrence may, therefore, require an interpretation similar to that which T. C. Chamberlin[1] makes for the fish of the Paleozoic, which he shows to have probably originated in the rivers and later become marine inhabitants, for geologic reasons becoming then abundant fossils. The Gastropoda may be immigrants to the marine habitat in Cambrian time. Assuming that there was a fresh-water molluscan fauna in Cambrian and Ordovician times, and that it is unknown to us, except as it is reflected in the early immigrants and in the preserved land and fresh-water faunas of later ages (Devonian to Recent), then we are able to explain some peculiarities of the Cambrian Gastropoda. From an ancestral gastropod stock in fresh water several immigrations to the sea may have taken place in Cambrian to Ordovician time, and that is what causes the emergence of new genera which we see in the marine fossils.

To illustrate from the region of the upper Mississippi valley, where the encroachment of the Cambrian Sea, as shown by Walcott, was in later Cambrian time, the oldest exposed strata are in the Dicellocephalus zone and of the Potsdam equivalent, and above this follows the Magnesian series, which is the Calciferous sand rock equivalent. Both have a known gastropod fauna; though it is necessary to offer a correction here, since inadvertently lists of fossils, such as that in *North American Geology and Palæontology* by S. A. Miller, refer species of the upper division only to the lower or Potsdam, and those of the "Potsdam" all to the upper division, which is the Calciferous or "Lower Magnesian," excepting *Hyolithes primordialis* Hall, which is rightly placed. Correctly referred, the faunas appear as follows: Associated with the brachiopod Lingulepis and the trilobites Agraulus and Dicellocephalus in the Dresbach formation occurs the *Hyolithes primordialis* Hall, widely distributed seaward, while at the seashore, as described, with it are the gastropods Tryblidium (Metoptoma), Hypseloconus, and Scævogyra. The succeeding Franconia sandstone, at Taylor's Falls, Minn., has the same genera of gastropods. This may be taken as the equivalent to the top of the Potsdam of New York.

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[1] JOUR. GEOL., Vol. VIII, pp. 400–412.

The next succeeding formation, the St. Lawrence, contains in a trilobite zone at Osceola, Wis., near Taylor's Falls and only a mile or two from the then seashore, *Tryblidium* sp.?, *Pleurotomaria sweeti* Whitf., *Murchisonia putilla* Sar., and *Bellerophon antiquatus* Whitif. At another point on the Blue Earth River, Minnesota, which is near another shore of that time, *Murchisonia putilla* Sar., was found either in the base of the Jordan sandstone, or as I suspect, now really the top of the St. Lawrence formation. Also *Raphistoma minnesotense* Owen and *Ophileta alturensis* Sar., occur in the same matrix. *R. minnesotense* Owen also comes from Red Wing, Minn., which is distant from the shore. Next, the coarse Jordan sandstone is practically the unfossiliferous basal sand of the Oneota dolomite, and this one is the supposed Lower Calciferous sand rock equivalent. Fossils generally have been obliterated in the Oneota, but a few Lingulas, and two fragments of trilobites, have been found, with a number of gastropods, which are the same species as those enumerated from the St. Lawrence formation, with also others of the genera Straparollus, Holopea, and Ophileta. Cephalopods also occur, of the genera Ascoceras, Piloceras, Orthoceras, *et. al.* The superjacent Shakopee dolomite (Upper Calciferous) contains only gastropods and cephalopods, as far as known, and, excepting the genus Subulites, they are species very similar to, though not identical with, those of the Oneota,[1]

In all these localities and horizons where the gastropods occur there are evidences of shallow water to be found, conglomerate, breccia, oölite, or mud balls. Rounded pebbles one or two inches in diameter occur even in the St. Lawrence formation of Red Wing, Minn. The species of fossils are quite all different from those of eastern America. Also the St. Peter sandstone (Chazy) has its peculiar molluscan species, but following this formation the Galena (Trenton) has numerous species which are largely identical with those from other regions, and surely of normal marine habitat.

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[1] F. W. SARDESON, "The Fauna of the Magnesian Series," *Bulletin of the Minnesota Academy of Natural Science*, Vol. IV (1896), pp. 92–105.

Thus in this region one appears to see the Gastropoda crawling off the rocks of the Cambrian seashore, migrating seaward, and becoming in Ordovician time the companions everywhere of the Brachiopoda and Trilobita, and this has suggested to me the probability of non-marine origin of Mollusca.

Such a theory does not change in any way the estimated imperfection of the geologic record as to the Gastropoda, except that the meaning of the same is differently taken when the ancestral stock is assumed to be the fresh-water fauna and not the salt-water one. The fresh-water and land faunas are totally unknown, and our Cambrian gastropods are immigrants, and thence the marine ancestors of Prosobranchia. The later emerging groups of Pulmonata and Ophistobranchia, for example, are not necessarily descended from the known Eo-Paleozoic, but would be descended from that unknown common stock. Cephalopoda may be derived from the first immigrated, widely found marine pteropodous genera Hyolithes, Hyolithella, etc. The class Pelecypoda, all but unknown in the Cambrian, might be taken as the third immigration seaward, and Scaphopoda the fourth. In this connection, I recall a former occasion for surprise when, in discovering Ordovician fossils in the St. Peter sandstone, I found that the Pelecypoda were both present and predominated, and Gastropoda and Cephalopoda were also in it. That formation is as unfavorable for fossils as any of the Cambrian fossil-bearing zones well could be, and therefore the Pelecypoda seem to have just arrived.

## THE EARLIER CAMBRIAN FAUNAS.

A review of the Cambrian representatives in the light of these theories may elucidate somewhat the phylogenic stage, whether primitive or whether advanced in Cambrian time. Walcott[1] describes about twelve species of gastropods in the Olenellus zone, or Lower Cambrian, and as many of the Hyolithoidea, or supposed pteropods. The Gastropoda include four species of Scenella (Plate I, Fig. 1) which are conical shells, about as high as wide; aperture elliptical or oval, tending to narrow posteriorly when the apex also inclines backward. The species are rather variable as described (*loc. cit.*), and in that respect not unlike the species of the Ordovician.[2] The genus apparently merges into the Patella of Silurian to Recent time, and is therefore of the Cyclobranchia as now known. Stenotheca (Plate II, Fig. 13) includes three species, distinguished from Scenella by concentric wrinkling of shell. A tendency in such shells toward curvature of the apex is worthy of note (*S. curvirostra* S. and F.). Platyceras, two species, includes *P. primaevum* Bill (Plate II, Fig. 14), which has a short, dextrally coiled apex or spire. The apex coils obliquely to the assumed dorsal direction. The aperture has the narrower side next the suture. *Straparollina remota* Bill (Plate II, Fig. 20) is a short dextral coil, with spire depressed and rounded in outline; whorls nearly uniformly rounded, more narrowly so on the upper side near the suture and also on the basal side. *Raphistoma attleboroughense* S. and F. (Plate II, Fig. 25) is a small dextral shell of three spiral whorls. These are rapidly expanding, closely coiled, and rather narrowly rounded on the outer side, which is a little thickened.

*Helenia bella* Walc. (Plate II, Fig. 17) is long, curved dorsally, and has an elliptical aperture, beveled toward the posterior. The apical end of it is imperfectly known. Similar to this one are the genera supposed to be pteropods. Hyolithes, including eight species, are long, conical, transversely broadened, anteriorly flattened, dorsally more or less angular, and the aperture is extended at the anterior side. There are sometimes apical loculi, and there is an operculum. In some there is a tendency to curve dorsally. Hyolithellus includes one species—a very long cone, or tubular. Coleoloides, one species, and Salterella, three species, of short tubular shells, complete the list as given by Walcott.

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[1] U. S. Geological Survey, *Tenth Annual Report*, pp. 616–25.

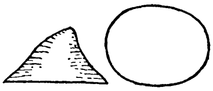
[2] The variability of Ordovician species of Scenella, Archinacella, etc., has been greatly underestimated by some authors.

The above species are very small shells, as compared to later ones like those of the Ordovician, and they were the kind to be the less easily and often fossilized because small and thin. There is little doubt that their small size and simple structure are truly representative of the earlier Cambrian marine Gastropoda of the Canadian and New England region.

The Baraboo fauna includes several species in three genera. Tryblidium (*Metoptoma* Whitf.) (Plate I, Figs. 2, 3) includes shells similar to Scenella, but the apex is more excentric and directed toward the narrower end of the oval or acuminate aperture, and the muscle scar is broken into distinct paired spots arranged in a circle or in horseshoe-shape, open anteriorly. In Hypseloconus (Plate I, Fig. 6) the apex rises posteriorly to the center, but by the curvature of the shell is directed forward. The muscle scars are apparently like those in Tryblidium. Scævogyra species (Plate I, Figs. 8, 9) are short, sinistral spiral coils. *Hyolithes primordialis* Hall is the accompanying pteropod. The western Upper Cambrian has therefore a primitive gastropod fauna similar to that of the eastern Lower and Upper Cambrian.

In interpreting these very simple types of gastropod shells there is noticeable difficulty at the start in choosing the right point of view. I have taken the generally oval aperture to be posteriorly acuminate and the apex as directed backward. In Scenella it ranges to anterior in position, but points rather backward because of a concave slope on that side of the shell. In Hypseloconus it rises posteriorly, but points forward. In other cases the curvature or coil may be assumed as backward directly or obliquely. There may have been a reason why the aperture was posteriorly narrowed. The animal is presumed to have been longer than wide, whence an oval shell could be well fitted to it, and, in case the shell rested back of the middle, the anterior of the shell might well be broader than the posterior, to accommodate the body at retraction. The curvature may be backward from some like simple cause. But in larger coils the

JOUR. GEOL., Vol. XI, No. 5 Plate I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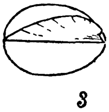
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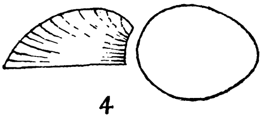
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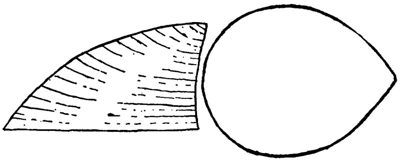
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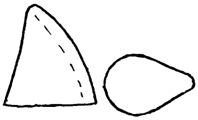
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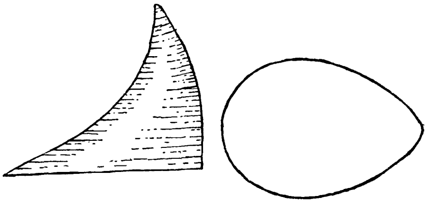
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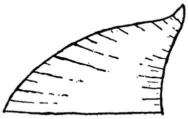
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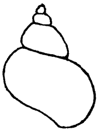
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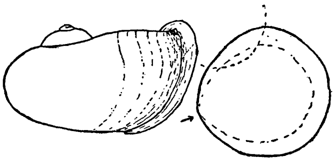
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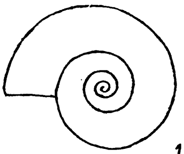
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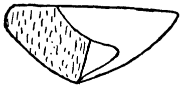
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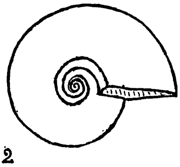
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FIG. 1, *Scenella reticulata* Bill., after Walcott; 2, *Tryblidium barabuense,* Whitf., × ½; 3, *Tryblidium simile* Whitf., × ½; 4, *Tryblidium nycteis* Bill., × ½; 5, *Tryblidium retrorsum* Whitf., × ½; 6, *Hypseloconus recurvum* Whitf., × ½; 7, *Metoptoma orithyia* Bill., × ½; 8, *Scævogyra sweezeyi* Whitf., × ½; 9, *Scævogyra elevata* Whitf., × ½; 10, 11, and 12, *Maclurea acuminata* Bill., after Whitfield, × ½.

same cause could not operate well because of change of poise or relation of shell to the body, and the acuminate aperture may not remain evident where the curvature has changed. The curvature may be taken as backward or lateral, and backward not forward, by rule, since the exception in Hypseloconus is seen to be a reversal (*vide H. recurva* Whitf., Plate I, Fig. 5). It is also notable that the Hyolithes curve backward when at all, and a reason for considering the angular side of Hyolithes as the posterior one may be deduced also from the triangular cephalopods. The initial of Endoceras is hyolithoid-shaped and angular dorsally; and, indeed, the frequent angular feature in early Cephalopoda, such as Gonioceras, and Triptoceras suggests that the oval acuminate aperture may have been ancestral. The cephalopod shell may have derived the marine hyolithoid species by formation of lateral loculi, in the manner described by Holm, in place of terminal ones, and the descent may have been in Cambrian time from Gastropoda to Hyolithoidea and to Cephalopoda, whence an ancestral trait of the oval aperture. Further, Cephalopoda and Hyolithoidea have not a coiled embryonic shell. Gastropods in the Cambrian should not, then, have, and are not known to have.

The curvature or coiling in the apex of the early Cambrian Gastropoda appears either equal to or greater than that in the maturer shell (*Platyceras primaevum*, Fig. 14), and correspondingly we may outline the morphologic series from that of the long conical to the apically curved, the apically coiled with curved base, and the entirely coiled, in accordance with the theory advanced, *i. e.*, that the shells of Cambrian time were coiling and not uncoiling. That these belong to an uncoiling stage would be tenable only on the evidence of an unknown fauna of spiral shells as old as, or older than, this one. Of that there is no proof. We do not know that there was a Cambrian larval spiral protoconch. In Recent shells such may have resulted altogether as it has in part since then. And, as said, the twisted mantle complex may have required no further cause than the shifting of a long cone. Taking the theory that the long conical shell, in Cambrian time, was ancestral to both the

JOUR. GEOL., Vol. XI, No. 5 Plate II

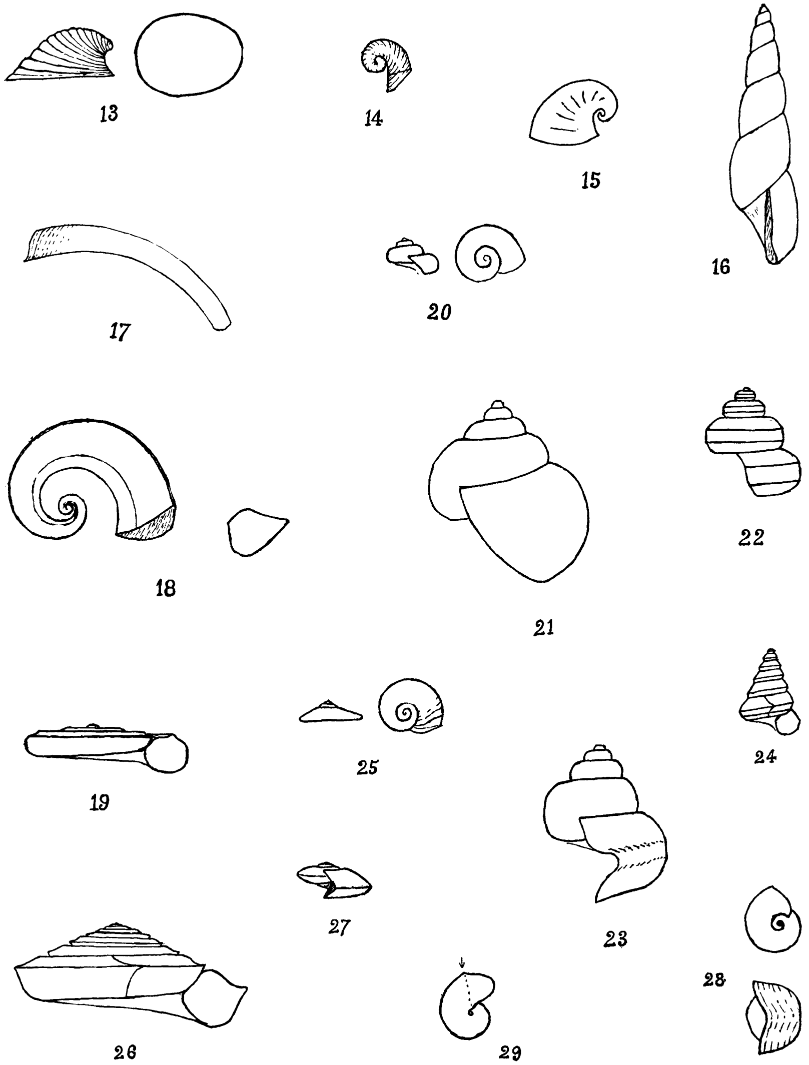

FIG. 13, *Stenotheca rugosa* Hall, after Walcott; 14, *Platyceras primaevum* Bill., restored, after Walcott, ×2; 15, *Platyceras primordiale* Hall, × ½; 16, *Subulites exactus* Sar., × ½; 17, *Helenia bella* Walcott; 18, *Ecculyomphalus triangulus* Whitf., × ½; 19, *Helicotoma similis* Whitf.; 20, *Straparollina remota* Bill.; 21, *Holopea obesa* Whitf., × ½; 22, *Trochonema exile*, Whitf.; 23, *Pleurotomaria sweeti* Whitf.; 24, *Murchisonia putilla* Sar.; 25, *Raphistoma attleboroughense* S. and F., ×4; 26, *Raphistoma minnesotense* Owen, × ½; 27, *Raphistoma leiosomellum* Sar., × ½; 28, *Owenella antiquata* Whitf.; 29, *Bellerophon vel Protwarthia*, × ½.

shorter cones and the spiral coils, the manner in which the spirals arose may be interpreted from the phenomenon seen in the Cambrian Gastropoda, where ontogenically the apex of the shell coiled most; and the conclusion is drawn that phylogenically the apex coiled first and the "body whorl" last. This is contrary to the view which has heretofore been held.

Possibly the example of uncoiling spiral shells in later geologic ages and the embryonic evidence of the Recent larval coiled shell have been applied too hastily to the interpretation of Cambrian Gastropoda. In the Cephalopoda the coiling is better known and affords fine examples for comparison. The correspondence of stages in phylogeny and ontogeny among the Ammonoidea, where the straight, curved, coiled, and uncoiled structure follow in order, is well known. In the Nautiloidea there very early occur both the coiling and the supposed uncoiling; and, indeed, there are such types as Ophidioceras, which is convolute in the middle and uncoiled at both ends. In this case the interpretation of the apical end as progressive and the apertural end as retrogressive might be taken as not sufficiently proved to serve as evidence. The Belemnoidean Recent genus Spirula is seen to have derived from a straight phragmocone, but is apically coiled, *i. e.*, it is in a genetic sense coiling, but appears uncoiling. After all, the Cephalopoda afford indecisive results, even if it was safe to apply a cephalopod measure to the grastropods. If anything fitting this case is indicated by them, it is that even within the group Gastropoda such uncoiling shells as Vermetus do not prove the rule.

The "Studies of Gastropoda"[1] by Grabau has come to hand after the above paragraphs were outlined and it may serve to indicate how firmly the view opposite to that here presented is held generally. Grabau unhesitatingly interprets *Platyceras primaevum* Bill., as a phylogerontic unrolled type.[2] He further cites Ordovician species as phylogerontic, following Ulrich's figures and descriptions in these, where, in the first instance, my collections lead me to conclusions widely different from those of Ulrich. We have to do with highly variable shells of fewer species than he describes. The "various degrees of uncoiling" are rather within a species in each case. That they are gerontic is, secondly, not assured.

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[1] *American Naturalist*, Vol. XXXVI, pp. 917–45.

[2] *Op. cit.*, p. 938.

Returning to the early Cambrian shells, the feature, in long cones, of the apical region coiling more than the maturer portion of the shell does is not necessarily to be interpreted as "uncoiling" in a genetic sense, but is as well or better to be considered as due to the curvature having set in at the apical region, and thence affecting the entire shell. Similarly, the reverse curvature is seen to affect the apex of *Tryblidium retrorsum* Whitf. (Fig. 5.), and the entire shell of *Hypseloconus recurva* Whitf. (Fig. 6), the former being then the transition from the normally curved long cones to the recurved short cones of the latter.

In all cases the change from straight to curved and coiled shell is accompanied by a change from directly transverse to obliquely cut back aperture in a very natural manner, as if the curvature of the shell preceded the elongation of the anterior, *i. e.*, the convexed side of the cone.

The next noteworthy feature is that, while the conical shells, which are very variable species, appear in each fauna, the coiled spiral shells are dextral in the eastern Olenellus fauna and sinistral in the Baraboo fauna. In this case the sinistral shells are evidently not sinistral derivatives of dextral ancestors by the depressing of the apex, as once suggested by Billings, below the median plane, since such transitions are unknown. A coiled intermediate type between the Raphistoma and the Scaevogyra does not appear, and coiling in bilateral symmetry was seemingly not yet developed or not yet immigrated. The link from the sinistral to the dextral shells may be interpreted as the known long conical type, and the two kinds of spiral shells as arising by parallelism. The sinistral might also be simply a mysteriously reversed form of the dextral, though they do not appear to be the sinistral individuals, or the near reverse of any dextral form, but relate rather to the retrorse long conical, Hypseloconus.

## THE CALCIFEROUS FAUNA.

The next succeeding fauna is in the Calciferous. This group may be considered as descended in main from the earlier types which are known to us, though a few are probably from unknown ancestors. In this Calciferous fauna there are, first, a number of short obtuse cones, of which *Tryblidium niobe* Bill. and *T. nycteis* Bill. (Fig 4) have the same general aspect as species of of the Baraboo fauna; *i. e.*, the shell smooth, curved with the apex overhanging the narrower end of the ovate aperture. The apex is, therefore, directed posteriorly, as I take it, though authors generally have designated the same as the anterior, because the line of paired scars of the type species were supposed to be open at this end, in a similar way as the continuous scar opens anteriorly in Patella. Ulrich and Scofield find otherwise for Tryblidium, and it may be better compared to Archinacella and Scenella, which have a continuous muscle scar which is not open anteriorly. These two genera occur also in the Calciferous zones. The one is low, smooth, conical, the other somewhat higher and ornamented, the apex being either central, or toward the broader, or toward the narrower end of the oval aperture. They, with Metoptoma (Fig. 7), may readily be taken to be the descendants of earlier species of Tryblidium, Hypseloconus, and Scenella, together comprising all such as have changed to shortened or lower cones, and they may be taken as tending toward the Patella, *et al.*, of more recent ages. Further, an interpretation of them might indicate that the apex is centrally or posteriorly directed, except in the Hypseloconus line, which would be the reverse of that, *e.g.*, *Metoptoma orithyia* Bill. (Fig. 7), and again that the broader end of the aperture is probably anterior.

Next to be mentioned is the genus Platyceras (Plate II, Fig. 15), which continues through and beyond the Calciferous zones, and is still intermediate between Stenotheca and the dextrally spiral shell type. Closest related to it is probably Holopea, but this is not clearly derived from it. Strangely enough, the division line between Diotocardia and Monotocardia, which so narrowly separates Scenella and Stenotheca, would also seem to divide the genus Holopea; or probably the Holopea-like species, when better known, may be found to be distributed between Holopea proper and Straparollus or a similar genus.

The Calciferous species of Holopea (Plate II, Fig. 21), Trochonema (Fig. 22), Straparollus, if the presence of this genus is conceded, and Raphistoma (Fig. 26), including *Raphistomina*, U. & S., are advanced little, except in respect to size, over earlier Cambrian dextral shells. They have the aperture simply formed, *i. e.*, cut obliquely from the sutural side (posterior) to the opposite (anterior) side. Holopea has rounded whorls, slightly impressed, forming a moderate spire with open umbilicus. Trochonema is similar, with angulations of the right or upper side of the aperture, producing keels on the whorls. Straparollus is a longer tube, coiled with wider umbilicus and more nearly discoid than Holopea. Raphistoma is low-coiled, with angulated anterior or periphery.

Other and associated types in the main may be viewed as modifications of these, by change of aperture and spire. In the case of these—to make a theory to fit the phenomena—there is a tendency in many species toward an extension of the apertural margin at the under outer side of the whorl, which produces a sinus, as in *Pleurotomaria* (*Seeleya*) *sweeti* Whitf.[1] (Fig. 23), which otherwise is like Holopea (Fig. 21.) Whether this apertural change is considered to be the building forward of certain parts or the cutting back of another, as writers generally have held of such shells, the species are in later time followed by others in which the change is more developed, the Calciferous species appearing to be midway in an evolutionary change which, in general terms, is a tendency to produce the aperture nearly in the plane of the shell's axis of coiling, *i. e.*, transverse to the volution. At the same time a notch is formed. The sinus in this case arises apparently not in front, but to the right side.

Closely related, though a link nearer to it may be shown, is the *Bellerophon* (*Owenella*) *antiquatus* Whitf. (Fig. 28), which is bilaterally symmetrical, since the spire is drawn in or sunken to the median plane of the volutions, and at the same time the aperture is built out below symmetrically, to form a broad sinus, which probably in this case was shifted to anterior, median of the animal. The genus or subgenus Protwarthia (Bellerophon) is also reported from the Calciferous. *P. cassinensis* Whitf. has the shell more rapidly expanding, (*i. e.*, shorter), the aperture larger, and the sinus narrower by reason of its sides projecting or building forward, as in the later *Bellerophon bilobatus* (Fig. 29). On the other hand, Oxydiscus, *e. g.*, *Bellerophon macer* Bill., while likewise bilaterally symmetrical, is convolute with abrupt umbilicus, and the aperture cuts obliquely backward, forming a wide sinus, the middle of which coincides with an angulation which is a keel peripheral to the volution.

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[1] *Holopea sweeti* Whitf. There can be no doubt that the specimens in hand are Whitfield's species.

A composite of these four genera and a transitional form from *P. sweeti* to the other three would be such as the species which I formerly described, as *Raphistoma leisomellum Sar.*[1] (Fig. 27), which consists of "about four rapidly increasing volutions, which embrace in such a manner as to form a lenticular coil," nearly equally convex above and below. The body whorl overlaps notably the periphery of the spire, though it is not a plain coil, the spire rising a little on the upper side, and an abrupt umbilicus, about one-fourth the width of the shell, being on the lower side. The periphery is narrowly rounded and slightly inflated, and the aperture is like those in Bellerophon and Pleurotomaria of the Calciferous.

Contemporaneous with and related to *P. sweeti* are a number of shells with high spires, in contrast to Bellerophon. They are comprised in the name Murchisonia *auct.*, or again under several generic terms—Lophospira, Clathrospira, Plethospira, Hormotoma, Cœlocaulus, and Tunitoma. These have a sinus, the abrupt middle of which produces a band upon the volutions, often coinciding with a keel (Fig. 24) or one of the keels. None of the species seem to have the sinus narrowed to a slit, as in the case of some of the later genera.

It may be true of these Murchisonia-like shells that the transition from a sinus to a slit has not yet been observed,[2] and this observation is not supplied here. The slit appears geologically later in species which logically seem to be the descendants of those which have the sinus. The view of Ulrich and Schofield, and Koken, that the sinus precedes the slit genetically is rather unavoidable, since apparently in Bellerophon, Pleurotomaria, *et. al.*, in later geologic time a slit appears where in shells of Calciferous age a sinus only occurs. There is, however, formed in species of Calciferous age a more or less distinct band by the more or less distinctly truncated bottom of the sinus. The building out of the apertural margin so as to narrow the sinus is in process of formation, though a "slit" would not be formed until the sinus is narrowed to the width of the band. The slit differs from the sinus in that growth-lines coincide upon its sides, as they were tending to do in the sinus, and a slit appears to have arisen from the sinus in several distinct genera, by parallelism of development. Further, the theory may be extended to the effect that the sinus, as seen in Protwarthia, Seeleya, Lophospira, *et al.*, is best explicable as the result of a genetically parallel development, their common ancestor having then had only its incipient stage developed. In the genera next to be mentioned here the presence of a sinus is not taken as evidence that the ancestor common to them and the preceding genera had other than a simple oblique shell aperture.

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[1] *Bulletin of the Minnesota Academy of Natural Science*, Vol IV (1896), p. 99.

[2] *Quarterly Journal of Geological Society*, Vol. LVIII, p. 317.

The low coiled shells, Helicotoma and Ophileta, have, therefore, been well united[1] with Straparollus in the family Enomphalidæ. The Straparollus has, of course, the obliquely cut aperture which I consider primitive. The other genera have the outer lip produced, making a sinus which as a rule coincides with a keel on the outer upper side of the whorls; and a band, when present, runs upon the keel. A slit has not been perfected in any of them. Helicotoma (Fig. 19) has the apex of the spire rather above the level of the elevated keel on the upper side. Ophileta has it rather lower, and the shell is less rapidly expanding than in Helicotoma. Another genus similar to these, Ecculyomphalus (Fig. 18), is coiled in one or more free volutions in nearly one plane. Authors generally have considered it an uncoiled shell, though it is better to regard it as coiling, showing a comparatively less rapidly developing retardation rather than retrogression. The existence of a well-developed sinus in view of parallelism of development does not argue that the shells are uncoiling. For the probable Lower Cambrian ancestral type of Ecculyomphalus, one may as well or better choose Helena (Fig. 17), a long curved cone, rather than the coiled Straparollina, since it is nearer the former in stage of coiling and equally far from both as to the aperture.

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[1] ULRICH AND SCHOFIELD, *Geological Survey of Minnesota*, Vol. III, p. 1023.

The genera which are referable to Montocardia in the Calciferous are Platyceras (Fig. 15) again and probably Holopea (Fig. 21) proper, the latter a symmetrical, short, spiral coil with primitive oblique aperture, reminding one of Straparollina, but much larger. With these, some species of high spiral shells, referred to the genus Subulites (Fig. 16) or somewhat uncertainly to Fusispira, emerge in the Calciferous. Like Holopea, they have no ornamentation, but a high, closely coiled spire, shallow sutures, and an elongated aperture. Between the straightness of the outer side and the impress of the preceding volution the sutural or posterior end of the aperture is narrowly acuminate. The apertural margin diverges from the simple obliquely backward course, or primitive aperture, by arching forward of this direction from the suture across the periphery, and then backward near the anterior end, and forward equally to the columella, making a neat sinus or canal at the anterior end.

It is unnecessary to more than mention the probable ancestral position of these Subulites shells in relation to the geologically later siphonate forms of the Monotocardia. The form of aperture in Subulites follows the tendency, herein suggested, to build forward from the obliquely and backward to the axially parallel direction, the difference from Pleurotomaria shells being in the position of the remaining notch, sinus, or canal, which is near the columellar instead of the peripheral margin.

In that way one can compare the Calciferous coiled shells with supposed primitive dextrally coiled Lower Cambrian ones with simple aperture, excepting in case of Maclurea (Plate I, Figs. 10, 11, 12), which is more difficult. If it is viewed as a dextral coil (Fig. 12), the spire, as Billings suggested, has sunk far below the median plane, in short, the umbilicus is then plane, the spire is reversed, and the aperture is then equally changed from the primitive obliquely backward position to somewhat obliquely forward. On the other hand, if it is viewed as a sinistral shell (Fig. 10) related to Scævogyra, the aperture runs then somewhat obliquely backward, and the narrower or posterior side of the aperture is at the umbilical margin (Fig. 11), as in that genus, to which the coil also corresponds, being more or less completely convolute (*vide M. speciosa* Bill.), though the spire's height is rather uniform. From what is known to me of Scævogyra, its species are considered to be rather greatly variable ones, and those of Maclurea, including Maclurina, are also not entirely constant. Even the great number of taxonomic species given by Ulrich (*op. cit.*) from the Galena is reduced to one species when a large number of specimens are examined. Comparison of immature specimens of Maclurea with Scævogyra will, I think, argue a close relationship between the two genera.

It is probable that Maclurea descended from Scævogyra, and that these are nearest to Hypseloconus and Tryblidium. Scævogyra does not occur after the Cambrian time, and, regarding later descendants of Maclurea, none are known, unless they become dextral shells. The mooted transitional forms or linking species between Ophileta and Maclurea in the Calciferous, if ever demonstrable, may be turned to argue the conversion of a primitive sinistral type to dextral Enomphaladæ, instead of inversely. The Enomphalidæ are, indeed, an ambiguous group, but whether, by reason of diverse origin of species, included in the family or not, does not yet appear.

Whether the Baraboo gastropods and Maclurea became extinct by dying out, or whether they have converged in part into other taxonomic groups, does not appear. They may be related to Recent Gastropoda in the manner of an offshoot from the ancestral fresh-water ancestors, and may be wholly extinct.

## THE ORDOVICIAN GASTROPODA.

The Ordovician gastropods next succeeding the Calciferous present an increased diversity, which is obviously an advance or continuation of the supposed development through Cambrian time It is unnecessary here to interpret it all in detail. Suffice it to note that in genera like Salpingostoma there is a maturity stage which was a new feature then in gastropod shells.

It will be useful to determine for the Ordovician species how much less constant they are in their characters than later gastropod faunas. There is danger of exaggeration, no doubt, if experience gained from a study of later Gastropoda is applied *a priori* to these earlier ones, since these may have the shell in a highly plastic stage, and seemingly great differences may not have a high taxonomic value. Such seems to me to be the case in studying large, carefully made collections, and accordingly I am inclined to desire a simplification of the taxonomic plan. In case of Pleurotomaria, both it and Bellerophon may have arisen from Raphistoma species, which argues close linking between these three. Again, Pleurotomaria may be from Raphistoma in part and from Holopea-like species in part; but this argues not only that the dividing up of Pleurotomaria, somewhat as Ulrich and Scofield have done, is logical, if practicable, but also that Raphistoma and Holopea-like species and their consequents are not genetically far apart. In case of Ordovician gastropod species, very excellent specimens are to be had in large numbers, at least in the upper Mississippi valley region, and these, when carefully studied, appear to show a high degree of variability. Ulrich and Scofield (*op. cit.*) have repeatedly based many taxonomic species on a few rather highly variable ones. The Ordovician fauna confirms the Cambrian shells to be rightly considered as little diverse, but variable to a high degree as compared with Mesozoic and recent probable descendants from them.

## CONCLUSION.

The early Cambrian Gastropoda are taken to be in an initial stage of differentiation, the amount of their evolutionary development at that time being represented by the change from a long curved conical to a short conical, on the one hand, and to short spiral coils on the other. The asymmetrical long conical shell is taken as the most primitive form among Cambrian Gastropoda, and the one from which the short conical shells, on the one hand, and the spiral and coiled shells on the other, have descended. Conical shells have arisen also from coiled and spiral ones in later geologic ages. The visceral twist probably correlates with the development of the long asymmetrical cone, or most primitive form, and not with the spiral shell.

The ancestor of the Mollusca was probably living in fresh water, and there the ancestral gastropods began. The Cambrian Gastropoda which are known to us appear to be immigrants to the sea, the fresh water and land stock remaining unknown to us geologically, though they may be reflected in the known marine immigrants. The Hyolithoidea may represent the first migration seaward. They comprise long conical, more or less curved, often triangular shells, and are the normal marine species, very probably representing the class Pteropoda; and from the same the Cephalopoda may have derived.

The second migration comprised the other Lower Cambrian Gastropoda. They are taken to be the ancestral group of Prosobranchia, and to be in process of change from long curved conical to short conical, on the one hand, and, on the other, to spirally coiled. The coiling is at the shell apex first and strongest; *i.e.*, the coiled form of mature shell arises by retardation. The aperture is simple and is oblique to the radius of the curve, or, in other words, the shell is not longest on the convex anterior side, for which reason the aperture runs obliquely backward from the inner (posterior) to the outer (anterior) side of the volution.

The gastropods in the Calciferous formations are readily interpreted as derived from the Lower Cambrian species, with certain exceptions. These are short conical shells, the Docoglossa. The Rhipidoglossa comprise species of long coils, with more or less changed aperture, which arises essentially by the building forward of the anterior or convex side of the shell, leaving near it a sinus in the margin, *e.g.*, Bellerophon, Pleurotomaria, and Murchisonia. These forms undoubtedly belong to Suborder 1, Diotocardia. To Suborder 2, Monotocardia, belong similarly Platyceras and Subulites, in the latter of which the aperture forms a shallow anterior canal.

The third immigration is that represented by the Baraboo fauna, with curved conical shells, retrorse shells, and sinistrally spiral ones. In the Calciferous there are the shorter cones, Tryblidium, and the sinistral spiral Maclurea. This group is somewhat problematical, being doubtfully Prosobranch and possibly Ophistobranch, recognizable species of Order II, Ophistobranchia, appearing first in the Devonian and Carboniferous, in the genus Actæonina. Order III, Pulmonata, at the same time appears in the genus Archæozonites and Dendropupa. Those three genera are primitive-looking, but of no recognized exact relation to any contemporaneous or preceding ones of the Prosobranchia among fossils; and it may be considered that their ancestors of Cambrian time were in the fresh-water fauna, from which also the Prosobranchia separated by migrating seaward in Cambrian time. The practically sudden emergence of marine Pelecypoda in the Ordovician time finally permits a theory of their freshwater origin, at that time, in accord with the view that Mollusca as a whole began in fresh water habitat.

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